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Natural History of the Bird-voiced  
Treefrog (*Hyla avivoca*) and Green  
Treefrog (*Hyla cinerea*) in Southern  
Illinois



Michael Redmer  
Lauren E. Brown  
Ronald A. Brandon

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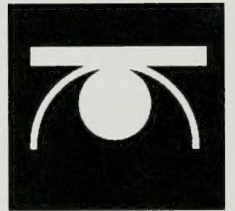
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## **Dedication**

This study is dedicated to the memory of our colleague, the late Dr. Michael A. Morris, with whom LEB initiated this project in the late 1980s as Mike completed his graduate work at SIUC. Mike was a foremost expert on the herpetofauna of Illinois and was associated with the Illinois Natural History Survey several times during his short career.

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# Natural History of the Bird-voiced Treefrog (*Hyla avivoca*) and Green Treefrog (*Hyla cinerea*) in Southern Illinois

The bird-voiced treefrog, *Hyla avivoca* Viosca 1928, Figures 1 and 2, and green treefrog, *Hyla cinerea* (Schneider 1799), Figures 3 and 4, are distributed primarily on the Atlantic and Gulf coastal plains of the southeastern United States (Conant and Collins 1998). The ranges of both species reach their northern limits in the Midwest in southern Illinois where Smith (1961) recorded them from Alexander, Jackson, and Union counties. Because the few documented localities of these treefrogs in Illinois were, until recently, mainly in or near remnant Austroriparian swamplands (which are disappearing rapidly), concern has been expressed that their continued existence in the state is in jeopardy (Ackerman 1975; Ashton et al. 1976; Dyrkacz 1974). Since Smith's (1961) comprehensive study *The Amphibians and Reptiles of Illinois*, few additional records for these species have been reported. Garton and Brandon (1975) studied reproductive ecology and habitat of *H. cinerea* at a southern Illinois swamp, but there has been no previous in-depth environmental examination of *H. avivoca* in Illinois. The objective of this publication is to report the results of our study of the natural history of these two poorly known treefrogs in southern Illinois.

## Materials and Methods

### Historical Records

Historical distributions were documented from published literature, unpublished reports, and museum specimens. Specimens were examined from the Field Museum of Natural History (FMNH), Illinois Natural History Survey (INHS), Illinois State Museum (ISM), Illinois State University (ISU), University of Kansas Museum of Natural History (KU), Lauren E. Brown Frog Collection (LEB), Louisiana State University Museum of Natural Science (LSUMZ), Michael A. Morris Collection

(MAM), Minton Herpetological Collection (SAM), Southern Illinois University at Carbondale Fluid Vertebrate Collection (SIUC), United States National Museum of Natural History (USNM), University of Illinois Museum of Natural History (UIMNH), and University of Michigan Museum of Zoology (UMMZ). See the Appendix for a detailed list of localities and preserved specimens examined.

### Current Distribution

Current distributions were determined in the field between 1961 and 1998 by listening for the species-specific mating calls and looking for individuals in vegetation and on roads in the vicinity of historic localities and other presumed suitable habitats. Most field work was carried out between May and August during and shortly after the chorusing seasons: May to mid-July for *H. avivoca* and mid-May to early August for *H. cinerea* (this study; Garton and Brandon 1975). Attempts usually were made to collect one or two voucher specimens (deposited at SIUC; Appendix).

### Habitat

Wherever we heard *H. avivoca* calling at night, we visited the localities again by day and recorded information on dominant tree species, including their condition (alive or dead), and understory species. In 1996 and 1997, perch sites of calling male *H. avivoca* were recorded at five locations: Heron Pond (NW 1/4 sec. 30, T13S, R3E), Hogan's Bottoms South (SE 1/4 sec. 23, T13S, R2E), Hogan's Bottoms North (NE 1/4 sec. 23, T13S, R2E), Bell Pond (NE 1/4 sec. 14, T13S, R4E), and Reevesville Swamp (NW 1/4 sec. 31, T13S, R5E). Type of perch, taxon if plant, and depth of water below each perch were recorded. Descriptions of habitat for *H. cinerea* are based on our field observations and information from the literature.





**Figure 1.** Female bird-voiced treefrog (*Hyla avivoca*) from Hogan's Bottoms (Cypress Creek drainage), Union County, Illinois. Photo by M. Redmer.



**Figure 2.** Tadpole of *Hyla avivoca* from Reevesville Swamp, Pope County, Illinois. Photo by M. Redmer.





**Figure 3.** Calling male green treefrog (*Hyla cinerea*) from Mermet Lake Conservation Area, Massac County, Illinois. Photo by M. Redmer.



**Figure 4.** Tadpole of *Hyla cinerea* from Reevesville Swamp, Pope County, Illinois. Photo by M. Redmer.



## Results

### *Hyla avivoca*

#### Description

*Hyla avivoca* is a moderately slender, small treefrog. Maximum reported snout-vent length (SVL) is 52 mm (Conant and Collins 1998). Males average smaller than females. The head is short with a truncate muzzle. The eyes are large and protuberant. Males have a subgular vocal pouch. The toe pads are conspicuous. The subarticular pustule of the fourth digit on the hand often (but not always) is divided by a furrow (Smith 1953). The hind toes are extensively webbed. There are a tarsal fold and two metatarsal tubercles (one small, one large) on each hind limb. The hand has one large (at the base of the thumb) and a number of small palmar tubercles. A fold of skin extends across the chest between the axillae. Another fold occurs across the dorsal aspect of the wrist. Dorsally the skin is relatively smooth, but ventrally it is granular. The background color of the dorsum is green, brown, or most frequently, various shades of gray. The venter is white or cream. Usually there is one large, irregular-shaped, dark blotch on the dorsum. One or sometimes two irregular dark spots occur between the eyes. A white spot (edged in black) is beneath each eye. The fore and hind legs have dark bars dorsally. A light green flash coloration occurs in the groin and on the posterior surface of the thighs.

The distinctive tadpole of *H. avivoca* (Fig. 2) was characterized by Altig (1970), Hellman (1953), Parker (1951), Redmer (1998), and Volpe et al. (1961). It has a mostly black body and tail with bold red, orange, or gold markings (saddles on the tail, interorbital and orbitonasal stripes).

The mating call of *H. avivoca* consists of a series of birdlike whistles. It was analyzed in detail by Blair (1958, 1959).

#### Comparison With Gray Treefrogs

There is a strong resemblance between *H. avivoca* and the gray treefrogs *Hyla chrysoscelis* Cope 1880 and *Hyla versicolor*

Le Conte 1825 in coloration and habitus. However, two features of live *H. avivoca* reliably distinguish them from *H. chrysoscelis* and *H. versicolor*: (1) the mating call of *H. avivoca* consists of a series of birdlike whistles whereas the mating calls of *H. chrysoscelis* and *H. versicolor* are trills with fast pulse rates; and (2) the light green flash coloration on concealed surfaces of the thighs of *H. avivoca* contrasts with yellow to orange flash coloration on the thighs of *H. chrysoscelis* and *H. versicolor*. Other characters sometimes are helpful in distinguishing *H. avivoca* from *H. chrysoscelis* and *H. versicolor* but do not provide absolute identification. For example, *H. avivoca* has a smaller size at maturation and smaller average adult size (Mecham 1960; Smith 1953, 1961). Also, *H. avivoca* has slightly smoother skin, and the subarticular pustule of the fourth digit of each hand often is divided by a furrow (Smith 1953, 1961, 1966). This pustule more often is undivided in *H. chrysoscelis* and *H. versicolor*. The tadpole of *H. avivoca* is, however, distinctive (see "Description") and contrasts with tadpoles of *H. chrysoscelis* and *H. versicolor*, which are olive green dorsally, white or cream ventrally, and sometimes have red or orange tails that lack bars (Altig 1970; Wright 1914).

#### Distribution

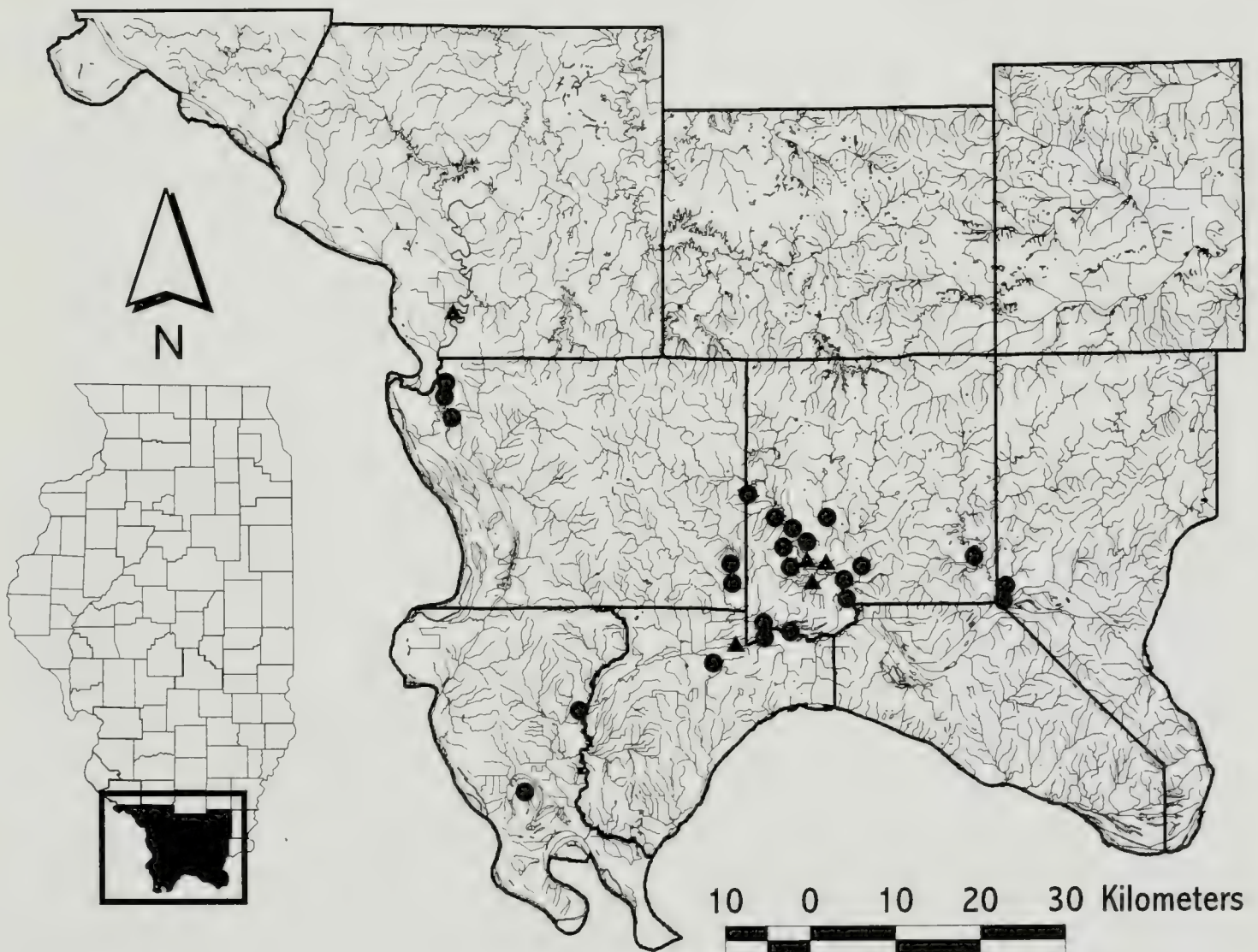
*Hyla avivoca* occurs in isolated colonies along the drainages of the Big Muddy River, Mississippi River, Cache River, and Bay Creek in Alexander, Johnson, Pope, Pulaski, Union, and possibly Jackson counties of extreme southern Illinois (Fig. 5, Appendix). However, before Smith's (1953, 1961) work, there was a question as to whether this species occurred in Illinois because of confusing nomenclature and strong resemblance of *H. avivoca* to frogs of the *H. versicolor* complex. Thirty-four years after Cope (1889) described *Hyla versicolor phaeocrypta* from Mt. Carmel, Wabash County, Illinois, Viosca (1923) described a distinct gray treefrog with a whistling call from Louisiana, which he tentatively identified as *Hyla phaeocrypta*. However, he noted that information on the mating call of Cope's



(1889) frog was lacking, so direct comparison with the frogs from Louisiana was not possible. Ridgway (1924) reported hearing birdlike whistles near Mt. Carmel, and speculated that this might have been the call of Cope's *H. phaeocrypta*. Viosca (1928) reconsidered his earlier report (1923) and named his treefrog as a new species, *Hyla avivoca*. He designated the type locality as Mandeville, Louisiana (holotype USNM 75017), and also identified a sample of 15 specimens of *H. avivoca* collected in 1907 from Olive Branch (= Horseshoe Lake), Alexander County, Illinois (FMNH 2201). We located and examined three of the specimens and confirm identification as *H. avivoca*. Nevertheless, a number of workers (Edgren 1953; Mittleman 1945; Neill 1948;

Parker 1951; and others) referred to the bird-voiced treefrog as *H. phaeocrypta* under the assumption that Cope's (1889) specimen from Mt. Carmel, Illinois, was conspecific and had priority. Smith (1953) clarified the identify of Cope's specimen as a member of the *H. versicolor* complex and demonstrated the proper application of *H. avivoca* as a distinctive treefrog, whose range included far southern Illinois, well south of Mt. Carmel.

Cagle (1942) reported a single specimen of *H. avivoca* (FMNH 25940) from Little Grand Canyon, Jackson County. This frog was sent to Karl P. Schmidt at the Field Museum of Natural History, Chicago, for identification (Cagle 1937). Schmidt (1937) identified the specimen (probably on the basis of its small



**Figure 5.** Distribution of *Hyla avivoca* in Illinois. Solid circles represent localities documented by voucher specimens examined or collected by us; triangles represent localities where we heard and/or saw specimens but collected no vouchers. Some plotted localities represent two or more nearby collection sites.



size) as *H. avivoca*, but added that it “requires the confirmation of additional specimens, and especially the check of hearing its peculiar birdlike whistle.” We examined FMNH 25940; it has undivided subarticular pustules on the fourth digits of the hands (as often is characteristic of the *H. versicolor* complex), and is a sexually immature male with a SVL of 31 mm. Mean SVL for 52 sexually mature preserved male *H. avivoca* from La Rue-Pine Hills Swamp/Wolf Lake is almost the same at 31.9 mm (range = 28-37), whereas the mean SVL for 41 sexually mature preserved male *H. chrysoscelis* from various localities in southern Illinois (the only species of the *H. versicolor* complex currently known to occur in the region; Appendix) is 36.4% greater at 43.5 mm (range = 38-49 mm). The two latter cohorts are obviously different because their ranges do not overlap. If FMNH 25940 were a *H. avivoca*, it should be sexually mature, which it is not. Thus, on the basis of size, sexual immaturity, and undivided subarticular pustules on the fourth digits of the hands, we conclude that FMNH 25940 was misidentified, and actually is a male of the *H. versicolor* complex (probably *H. chrysoscelis*). However, it is quite probable that *H. avivoca* does occur just west of Little Grand Canyon at Oakwood Bottoms (see information that follows).

Between 1961 and 1991, *H. avivoca* was reported or documented from Alexander, Johnson, Pulaski, and Union counties (Brandon and Morris 1987; Brown and Pierce 1965; Klimstra and Hutchison 1965; Smith 1961, 1966). Since then, we have found a number of populations in Alexander, Jackson, Johnson, Pope, Pulaski, and Union counties (Fig. 5; Appendix). Brandon and Ballard (1997) inadvertently included Massac and Williamson counties within the known range of *H. avivoca*. However, there are no known vouchers, and we have been unable to locate choruses.

In the Bay Creek drainage, *H. avivoca* is common at Bell Pond (= Grantsburg Swamp of Mohlenbrock 1991), although previously recorded there only by Brandon and Morris (1987). We heard large choruses from 1993 through 1996 and collected a voucher (SIUC

H-4741). In 1996 we found large populations in two small swamps east of Reevesville, Pope County (Redmer 1998) ca. 13 km downstream (ca. 6 km straight-line distance) from Bell Pond, and collected vouchers (SIUC H-5251-5253, H-5383-5385, H-5543, H-5598).

Most of the known records in Illinois are in the drainage of the Cache River, including three of its tributaries (Cypress Creek, Dutchman Creek, Limekiln Slough). *Hyla avivoca* was reported earlier in this drainage by Klimstra and Hutchison (1965), Evers and Page (1977), and Brandon and Morris (1987, 1988). Localities have been found from as far upstream as Cypress Pond State Natural Area at the Union/Jackson county line near the town of Mt. Pleasant (Appendix), and as far downstream as east and south of Tamms, Alexander County (Burbrink et al. 1995, 1998). Along the nearly 80 km of stream between these sites, suitable habitat is fragmented by drainage projects, channelization, timber clearing, and natural topography. In Heron Pond-Little Black Slough State Natural Area, *H. avivoca* may be continuous over a broad expanse of baldcypress (*Taxodium distichum*)/tupelo (*Nyssa aquatica*) swamp. Because much of this natural area is relatively remote and inaccessible, and part of it (Heron Pond) is protected as an Illinois Nature Preserve, preserved specimens from this 6,000-hectare area are uncommon in museum collections. In addition to four sites represented by voucher specimens, we heard choruses at two additional sites within this swamp.

*Hyla avivoca* has been collected infrequently at Horseshoe Lake, Alexander County. We located and examined three of the specimens of *H. avivoca* (FMNH 2201) that Viosca (1923, 1928) reported from Olive Branch (actually collected at Horseshoe Lake [Viosca 1923]) and agree with his identification of them as *H. avivoca*. An immature specimen (SVL = 26 mm; LSUMZ 51046) collected from Horseshoe Lake by D. Rossman in 1957 was identified by him as *H. avivoca*. No information on flash coloration is available for this specimen, nor is it known whether Rossman heard breeding choruses. However, the



subarticular pustules on the fourth digits of the hands are undivided (more often characteristic of the *H. versicolor* complex). At present we do not feel there is enough evidence on hand for us to justify species identification of this specimen. LEB never found *H. avivoca* at Horseshoe Lake over his many years of field work there dating back to 1961. Furthermore, intensive field work in the area from 1986 to 1996 (Brandon 1994; Brandon and Morris 1987, 1988; Brandon and Wilson 1996; Heidinger et al. 1994, 1995) did not uncover the species in what is now greatly disturbed habitat (discussion follows). Thus, *H. avivoca* may be extirpated at Horseshoe Lake.

In the drainage of the Big Muddy River, *H. avivoca* is common and well documented in the literature at La Rue-Pine Hills Swamp/Wolf Lake, Union County (Ballard 1994; Brown and Pierce 1965; Evers and Page 1977; Minton and Minton 1948; Rossman 1960; and Smith 1953, 1961). In 1992, one of us (MR) heard a calling male at Worthen Bayou, Oakwood Bottoms-Turkey Bayou Waterfowl Management Area, approximately 1.5 km southwest of Cagle's (1942) Little Grand Canyon locality. Michael Morris (pers. comm.) also heard *H. avivoca* at Oakwood Bottoms. We have heard none in recent years, but flooding during late May and early June prevented visits to the site in 1995 and 1996.

An immature specimen (SVL = 22 mm; LSUMZ 51047) was collected in 1957 by D. Rossman at Union County Conservation Area and identified by him as *H. avivoca*. This frog is faded and the subarticular pustules on the fourth digits of the hands are undivided (more often characteristic of the *H. versicolor* complex). No information on flash coloration or mating call is available, so we cannot justify identifying it to species. We visited Union County Conservation Area many times during 1991-1997, but never heard *H. avivoca*.

### Habitat

We found *H. avivoca* only in or on the edges of remnant swamps dominated by baldcypress or tupelo gum along rivers and streams. An example of this type of habitat, La Rue-Pine

Hills Swamp/Wolf Lake, was described in detail by Mohlenbrock (1959). Voigt and Mohlenbrock (1964) termed these communities "deep swamps." They are characterized by water fluctuating from less than 2 cm in summer to as much as 1.5 m in winter. Voigt and Mohlenbrock's (1964) map showing distribution of these deep swamps in Illinois and Mohlenbrock and Ladd's (1978) map of the range of *N. aquatica* in Illinois both roughly parallel the range of *H. avivoca*. Other trees commonly associated with these swamps are water hickory (*Carya aquatica*), pumpkin ash (*Fraxinus tomentosa*), water locust (*Gleditsia aquatica*), and swamp red maple (*Acer drummondii*). Common understory plants include buttonbush (*Cephalanthus occidentalis*), swamp rose (*Rosa palustris*), and swamp loosestrife (*Decodon verticillatus*). While baldcypress and tupelo gum commonly occur together in these swamps, mature stands of one species often nearly exclude the other. Voigt and Mohlenbrock (1964) noted that baldcypress-tupelo gum communities or tupelo gum alone dominate in deep water, and that baldcypress-pumpkin ash communities dominate where water is less than 0.3 m deep.

Little has been reported previously about the habitats of *H. avivoca* in Illinois. During field work in 1996 and 1997 (when all known localities in Illinois were examined), we found large choruses (>10 or more individuals calling) only in pure or mixed stands of baldcypress and tupelo gum (Fig. 6A), or in adjacent reed thickets (*Phragmites australis*, Fig. 6B). Where the swamp canopy was dense and the understory diverse and well shaded by day, *H. avivoca* usually was the dominant calling anuran (other species calling included cricket frogs, *Acris crepitans*; bullfrogs, *Rana catesbeiana*; green frogs, *Rana clamitans*; and occasional *H. cinerea*). Few calling *H. avivoca* (< 5 individuals) were present in more open shrubby wetlands (Fig. 7A), or where baldcypress and tupelo gum were sparse, immature, or appeared stressed or dying (Fig. 7B). Sometimes none were seen or heard in such open areas on nights when large choruses were heard at adjacent shaded swamps.



**A**

**Figure 6.** Habitats of *Hyla avivoca* in Illinois as they appeared in August. A (Top): Mature baldcypress-tupelo swamp 1.5 km NE Reevesville, Pope County. B (Bottom): Reed thicket adjacent to the above swamp (this was the only place where tadpoles of *H. avivoca* were collected during this study). Photos by M. Redmer.

**B**





**A** **Figure 7.** Habitats of *Hyla avivoca* and *Hyla cinerea* in Illinois as they appeared in August.  
A (Top): Open-water buttonbush-cattail swamp adjacent to mature baldcypress-tupelo swamp 1.5 km NE Reevesville, Pope County. B (Bottom): Declining baldcypress-tupelo swamp at Hogan's Bottoms 3.4 km W Cypress, Union County. Photos by M. Redmer.





Usually *H. cinerea* was dominant in these open wetlands where *C. occidentalis* was common.

Fifty-five male *H. avivoca* called from ten species of plants, dead logs (not identified to species), and the metal rail of an interpretive trail. Perch species or type (and frequency of use) were as follows: *N. aquatica* (23.6%); *T. distichum* (21.8%); *C. occidentalis* (16.4%); *A. drummondi* (9.1%); *Rosa palustris* (7.3%); *P. australis* (7.3%); metal rail (5.5%); *F. tomentosa* (3.6%); Virginia willow, *Itea virginica* (3.6%); and floating log (1.8%). Fifty-three frogs were 0.1–2.3 m (mean = 1.5 m) above water. Two perched on vegetation rooted in soil along the swamp margin. One frog was observed calling on the trunk of a tupelo 3 m above water. (On other occasions we observed *H. avivoca* calling on perches >3 m above water.) Water depths below 53 emergent perch sites were 0.1–0.7 m (mean = 0.3 m).

At Reevesville Swamp, 13 tadpoles of *H. avivoca* were collected on 7 and 10 July 1997. All were netted from shaded water (< 0.3 m deep) below the interior of a thicket of *P. australis*. Other attempts to collect tadpoles of *H. avivoca* were unsuccessful, despite repeated daytime searching at known chorus sites and habitats (especially around bases of tupelo and baldcypress trees).

We occasionally found recently metamorphosed juveniles in late summer or early autumn, after the breeding season. Most were observed perched in low (< 2 m) shrubs in woodlands adjacent to swamps where breeding choruses had been observed previously. On 25 April 1996, MR observed five subadults, one adult male, and an adult female prior to the breeding season, all perched on low emergent vegetation and on trunks of baldcypress and tupelo gum trees. However, on 30 September 1995 and 20 September 1996, LEB and MR found one adult and several subadults on the ground and perched in low vegetation in the forest adjacent to Heron Pond. LEB found terrestrial subadult *H. avivoca* adjacent to Reevesville Swamp and La Rue-Pine Hills Swamp on 26 September 1998. Rossman (1960) also noted the terrestrial tendencies of the species in autumn at Pine Hills Swamp.

## *Hyla cinerea*

### Description

*Hyla cinerea* is a moderately large treefrog with a slender, elongate body. Maximum reported SVL is 64 mm (Conant and Collins 1998), with males averaging smaller than females. The head is flat and the snout is pointed. Males have a subgular vocal pouch. The toe pads are conspicuous and the hind limbs are long. Extensive webbing occurs between the hind toes. There are two metatarsal tubercles (one large, one small) and a tarsal fold on each hind limb. On each hand there are one large (at the base of the thumb) and a number of small palmar tubercles. A fold of skin occurs across the chest between the axillae. Another fold extends dorsally across the wrist. Dorsally the skin is smooth but ventrally it is granular. The dorsum usually is bright green, but sometimes olive or yellow-green. Small gold flecks that frequently have a black border often are scattered on the dorsum. A white lateral stripe extends from the snout, beneath the eye, to midbody or nearly the groin. This stripe sometimes is broken but rarely is absent. The venter is white or cream. Dickerson (1907, p. 127) wrote: "The Green Tree Frog is perhaps the most beautiful tree frog in North America."

The tadpole of *H. cinerea* (Fig. 4) has yellow orbitonasal stripes, a greenish body (dorsally and laterally), yellow tail with dark reticulations, and yellow or buff venter (Altig 1970; Wright 1932).

The loud and distinctive mating call (Blair 1958, 1959) of *H. cinerea* is best described as a nasal "frank, frank, frank. . ." Large choruses (e.g., at La Rue-Pine Hills Swamp/Wolf Lake) produce a tremendous cacophony that can be heard 1–2 km or more away.

### Distribution

*Hyla cinerea* is widely distributed across much of extreme southern Illinois in Alexander, Jackson, Johnson, Massac, Pope, Pulaski, Randolph, Union, and Williamson counties (Fig. 8; Appendix). The first record in southern Illinois (no specific locality) probably was



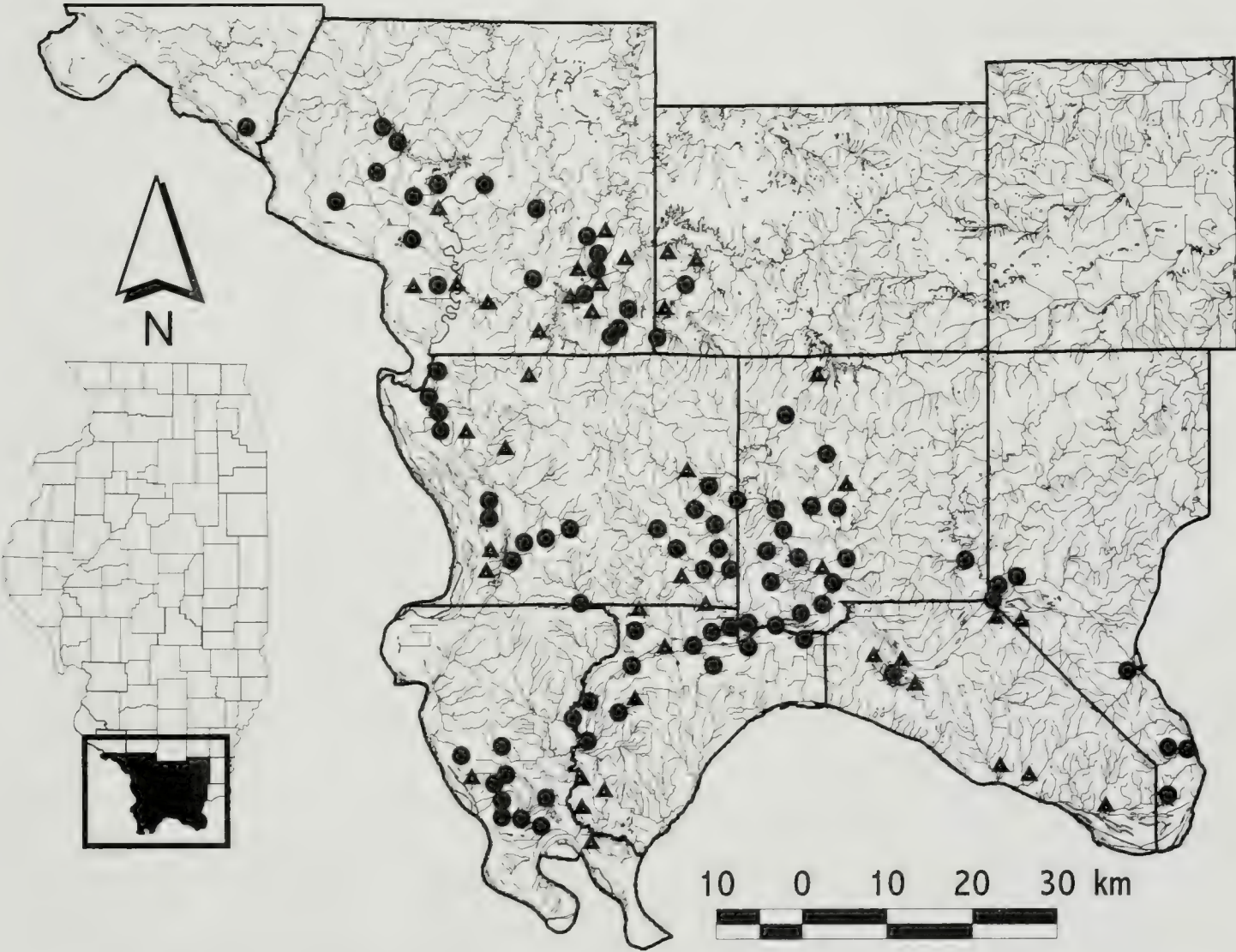
provided by Davis and Rice (1883), who identified them as squirrel treefrogs *Hyla squirella* (a similar species found in the southeastern U.S.). Garman (1890, 1892) subsequently reported them from Bluff Lake, Union County.

Additional valid records (Fig. 8; Appendix) of *H. cinerea* in Illinois include La Rue-Pine Hills Swamp/Wolf Lake, Union County (Ballard 1994; Brown and Pierce 1965; Cagle 1942; Garton and Brandon 1975; Minton and Minton 1948; Rossman 1960; Smith 1961), several localities in Johnson County (Brandon and Morris 1987; Klimstra and Hutchison 1965; Phillippi et al. 1986), in Pulaski County (Brandon and Morris 1987), and in Massac, Pope, and Williamson counties (Redmer and Ballard 1995). In all of these counties we found numerous additional localities. We report it for the first time in Jackson County

(although it was documented there by museum specimens collected as early as 1980) and Randolph County (Fig. 8; Appendix).

In the late nineteenth century, two localities were reported for *H. cinerea* far north in the vicinity of St. Louis. Because these northern records are of highly questionable validity, it is pertinent to discuss them in detail.

A single specimen of “*Hyla Carolinensis*” (= *H. cinerea*) was found at “Cantine [*sic*] Creek, Cantine [*sic*], Madison County, Ill.” by the pioneer Missouri herpetologist Julius Hurter (1893), who spent considerable time in the vicinity of St. Louis. He did not mention this specimen in later publications (1897, 1903, 1911) on the herpetofauna of Missouri, but there is no doubt that he was familiar with *H. cinerea*, as evidenced by his collection of other specimens of the species (USNM 57732, 57736) in Alabama and Louisiana in 1892. We



**Figure 8.** Distribution of *Hyla cinerea* in Illinois. Solid circles represent localities documented by voucher specimens examined or collected by us; triangles represent localities where we heard and/or saw specimens but collected no vouchers. Some plotted localities represent two or more nearby collection sites.



contacted T. Johnson (an authority on the herpetofauna of Missouri), who indicated that most of Hurter's specimens were deposited in the U.S. National Museum of Natural History, with some going to the Chicago Academy of Sciences and the Academy of Science of St. Louis (antecedent of the St. Louis Science Center). Johnson also indicated that Hurter's field notes may be located at these institutions or the Naturalists Club in St. Louis. No specimens of *H. cinerea* from Illinois collected by Hurter or any of his pertinent field notes are located in the Chicago Academy of Sciences, St. Louis Science Center, or Naturalists Club (R. Vasile, R. Beer, R. Goellner, pers. comm.). However, the U.S. National Museum of Natural History has a specimen (USNM 57827) collected by Hurter on 1 May 1892 in Madison County, Illinois. (No additional information is available on the locality [G. Zug, pers. comm.].) We have examined this juvenile male (SVL = 25 mm). Although the color pattern is faded, white spots can still be detected under the eyes, and the subarticular pustules on the fourth digits of the hands are undivided (as is often characteristic of the *H. versicolor* complex). We conclude it is a member of the *H. versicolor* complex. (*Hyla avivoca* also has white spots under the eyes, but the northern collection locality makes it unlikely that USNM 57827 is of that species.) Young frogs of the *H. versicolor* complex frequently are light green dorsally (Dickerson 1907), and superficially similar to *H. cinerea*. Thus, Hurter (1893) may have misidentified the young specimen of the *H. versicolor* complex (USNM 57827) as "*Hyla Carolinensis*" (= *H. cinerea*). We contacted R. Axtell, herpetologist at Southern Illinois University at Edwardsville, about the possibility of *H. cinerea* occurring in Madison County. In his many years of field experience in that area he never collected any, nor is he aware of anyone else who has encountered the species in Madison County. In June 1995 and July 1997 we searched for *H. cinerea* in the vicinity of Canteen in southern Madison County and St. Clair County. None were heard or seen, but a small chorus of *H. versicolor* was heard near Canteen Creek.

Cope (1889) reported two specimens of *H. carolinensis* (both under USNM 1070) collected by George Engelmann from St. Louis. This collection locality is pertinent to our study because it lies just across the Mississippi River from Madison County, Illinois. R. Crombie and R. Reynolds of the U.S. National Museum of Natural History provided us with the following information pertaining to USNM 1070 (as well as subsequent specimens discussed). Cope had the bad habit of cutting off the tags of hundreds of specimens he borrowed from the U.S. National Museum of Natural History. He later reassociated tags and specimens, some correctly, many incorrectly. After Cope died, many specimens were returned to the U.S. National Museum of Natural History without tags. To further complicate the issue, in the earlier years at the U.S. National Museum of Natural History it was a standard practice to assign a single catalogue number to a lot of specimens from a single collector. When a lot was recognized as containing more than one species, the extra species was recatalogued. Presently USNM 1070 is assigned to a water snake (*Nerodia*) as are all those numbers surrounding 1070. Interestingly, 1070 was received from Engelmann and was from St. Louis. There is nothing to suggest (other than Cope 1889) that 1070 was ever associated with any frogs. No further information is available on 1070 or any other possibly associated frogs.

Other frogs of pertinence in the U.S. National Museum of Natural History include USNM 3667 (four specimens) and 104553 (one specimen), which were collected by Engelmann from St. Louis and entered into the catalogue in 1858. These specimens are all of the *H. versicolor* complex. USNM 3667 is listed by Cope (1889) under *H. versicolor*, but as one specimen rather than four. USNM 104553 originally was catalogued as USNM 3453 (also listed by Cope [1889] as *H. versicolor*). USNM 3453 was a lot also containing two wood frogs (*Rana sylvatica*), which retained the original number, while the member of the *H. versicolor* complex was recatalogued in 1938 as USNM 104553. There is no reason to



assume that USNM 3667 and/or 104553 were the specimens Cope (1889) referred to as *H. carolinensis* (= *H. cinerea*) USNM 1070 from St. Louis. Furthermore, Johnson (1987) found that the farthest north that *H. cinerea* occurs in Missouri along the Mississippi River is well to the south in Cape Girardeau County (across the river from Union and Alexander counties, Illinois).

We conclude that there is no compelling evidence that the nineteenth century records of *H. cinerea* from Madison County, Illinois, and St. Louis, Missouri, are valid.

### Range Expansion

It became apparent to us that *H. cinerea* expanded its range northward and eastward in Illinois during the past 10–25 years. LEB carried out field work in southern Illinois as a graduate student at Southern Illinois University in the early 1960s and never observed *H. cinerea* in or near Carbondale, Jackson County. RAB has lived in Carbondale and carried out field research in the area for over 30 years and never encountered *H. cinerea* in the vicinity of Carbondale before the 1980s. In 1982, M. Morris (pers. comm.) was the first to find *H. cinerea* in Carbondale at Evergreen Park. He continued to encounter the species there through 1987. In the late 1980s, W. McDowell (pers. comm.) collected *H. cinerea* from a sewage lagoon (Fig. 9A) on the south edge of Carbondale, and a large colony continues there now. Additional large colonies were discovered at other sites on the south edge of Carbondale and on the campus of Southern Illinois University at Carbondale during 1991 and 1994–1997. These were discovered in a generally south to north order over successive years, possibly indicating a gradual invasion of suitable breeding habitat in Carbondale. During 1995–1997, *H. cinerea* was heard and collected in the drainage of Drury Creek and in ponds as well as along the road in Giant City State Park near Boskydell and Makanda. Drury Creek passes the southeastern edge of Carbondale (within 1.2 km of the sewage lagoon) in its flow northward to Crab Orchard

Creek and the Big Muddy River. Thus, *H. cinerea* from Drury Creek may have colonized Carbondale during the past 20 years. At least one Austroriparian reptile (the cottonmouth, *Agkistrodon piscivorus*) has been collected in the drainage of Drury Creek. Additional colonies of *H. cinerea* have been found since 1991 in southeastern Jackson County, mostly in retention ponds or lakes not far from Drury Creek.

In 1995 and 1996 large choruses were observed in ponds at two commercial fish farms (Fig. 9B) on the floodplain of the Mississippi River in western Jackson County. Both fish farms are within 1.5 km of floodplain swamps containing *H. cinerea*. The species also occurs in weedy bays of Little Grassy Lake (Fig. 10A) less than a km from the Little Grassy Fish Hatchery (operated by the Illinois Department of Natural Resources) along the Williamson and Jackson county line. The fish hatchery is in an upland setting ca. 4 km from the nearest natural wetlands with a colony of *H. cinerea*.

Choruses have been observed and documented in most of the medium to large lakes in far southern Illinois, all of which were impounded in this century. These include (with impoundment dates) campus lake at Southern Illinois University at Carbondale (impounded twice, in slightly different basins, most recently ca. 1952), Carbondale Reservoir (ca. 1925), Cedar Lake (ca. 1973), Crab Orchard Lake (ca. 1940), Dutchman Lake (ca. 1973), lake at Ferne Clyffe State Park (ca. 1960), Kinkaid Lake (ca. 1971), Lake of Egypt (ca. 1962), Little Grassy Lake (ca. 1940), and Lake Murphysboro (ca. 1970). Most of these are deep (over 5 m) upland reservoirs, many have clear water, and many have limestone or sandstone ledges along portions of the shoreline. All have shallow bays with abundant emergent vegetation (Fig. 10A). Choruses of *H. cinerea* usually occurred in eutrophic heads of shallow bays where cattail (*Typha* sp.), willow (*Salix* sp.), American lotus (*Nelumbo lutea*), and other emergent plants were abundant.



**A**

**Figure 9.** Habitats of *Hyla cinerea* in Illinois as they appeared in August. A (Top): Sewage lagoon at a mobile home park, Carbondale, Jackson County. B (Bottom): Commercial fish farm ponds 1.2 km E Gorham, Jackson County. Photos by M. Redmer.

**B**



**A**

**Figure 10.** Habitats of *Hyla cinerea* in Illinois as they appeared in August. A (Top): Weedy bay of Little Grassy Lake at Giant City State Park, Jackson/Williamson counties. B (Bottom): Morgan Pond, a karst sink pond ca. 3 km E Dongola, Union County. Photos by M. Redmer.

**B**



### Habitat

We found *H. cinerea* in a wide variety of wetland habitats. All chorusing sites were sunlit by day because tree canopy was sparse or absent. Male *H. cinerea* usually were observed calling from elevated perches in *N. lutea*, *Typha* sp., shrubs (especially *C. occidentalis*), or young trees (especially *Salix* sp.). Dense mats of duckweed (mostly *Lemna* sp.) were present at most localities. Many of these habitats appeared disturbed or successional because mature baldcypress and tupelo gum trees (if present) usually were dead or stressed, and shrubs (especially *C. occidentalis*) were abundant (Fig. 7A, B). Furthermore, the dominance of *Typha* sp. at a number of the sites is indicative of habitat disturbance (Anderson and Brown 1991; Odum 1988). Phelps and Lancia (1995) found *H. cinerea* in South Carolina more abundant in clearcut swamp than

in a nearby timbered swamp. In eastern Union County, choruses often were found in karst sink ponds (Fig. 10B) and farm ponds. Emergent vegetation in these habitats sometimes consisted of *N. lutea*, *Typha* sp., *C. occidentalis*, and *Salix* sp., but a few such ponds were located in pastures and crop fields where emergent vegetation consisted of crop plants or stubble. Impoundment lakes in southern Illinois often have rocky, steeply sloped shorelines (Harris et al. 1977), which do not offer suitable habitat for *H. cinerea*. However, these lakes usually are fed by many small tributary streams that deposit sediment into bays (Harris et al. 1977). Consequently, the shallow bays become heavily vegetated (Fig. 10A) and provide suitable habitat for *H. cinerea*. In addition to the various impoundment reservoirs, we also found choruses of *H. cinerea* in several borrow-pit ponds along roads (Fig. 11).



**Figure 11.** Habitat of *Hyla cinerea* in Illinois as it appeared in August: Shallow borrow pit pond along Interstate 24, 1.4 km SW Big Bay, Massac County. Photo by M. Redmer.



The habitat at Otter Pond, La Rue-Pine Hills Swamp/Wolf Lake was described by Garton and Brandon (1975), where they found males usually called from branches or leaves of several emergent plants including *Rosa palustris*, *C. occidentalis*, *D. verticillatus*, and yellow pond lily (*Nuphar advena*), usually 0.3 m or more above water. During peak breeding, calling males were also found on perches nearer water (within 0.2 m) and on mats of surface vegetation.

We found tadpoles to be abundant in warm (sunlit) water at breeding sites. The tadpoles (usually with tadpoles of cricket frogs, *A. crepitans*) were most often found in shallow (< 20 cm deep) water and under mats of duckweed.

During September–October, we frequently found recently transformed *H. cinerea* in emergent vegetation and shrubs around the peripheries of breeding sites, and even in grassy fields. Garton and Brandon (1975) as well as this study found that young-of-the-year moved into surrounding floodplain and adjacent upland forest by September and October. Some may have spent the winter under limestone talus or in rock crevices.

## Discussion

### Biogeography

Because both *H. avivoca* and *H. cinerea* are Austroriparian species that reach their northern limits in Illinois, their biogeographic histories in the state have much in common. Remnants of the baldcypress/tupelo gum swamplands that formerly were extensive across far southern Illinois now are concentrated mostly in three areas: (1) the floodplain of the Mississippi River and drainage of the lower Big Muddy River; (2) the drainages of Bay Creek, Cache River, and former channel of the Ohio River in which swampland was extensive before being largely drained for agricultural purposes (Alexander and Prior 1968; Hutchison 1987); and (3) the lowlands of southern Massac and Pope counties adjacent to the Cretaceous Hills Section, which drain directly into the Ohio River (Harris et al. 1977).

*Hyla avivoca* usually is described as an inhabitant of large forested swamps along rivers (Blair and Lindsay 1961; Conant and Collins 1998; Dundee and Rossman 1989; Krupa 1986; Trauth and Robinette 1990; and others). In Illinois, all localities are floodplain swamps in drainages of Bay Creek, Big Muddy River, Cache River (and its tributaries Cypress Creek, Dutchman Creek, and Limekiln Slough), and (formerly) Lake Creek. One of these (Big Muddy River) is a tributary of the Mississippi River, while the remainder are tributaries of the Ohio River.

*Hyla avivoca* probably originally invaded southern Illinois by moving northward up the Mississippi embayment. The populations along the Big Muddy River, lower Cache River, and Mississippi River are a direct result of that colonization. However, the biogeography of *H. avivoca* along the upper Cache River and Bay Creek requires a more complex interpretation. The swamps along these rivers are remnants of the floodplain habitat of the ancient channel of the Ohio River. This channel cut across (from east to west) large parts of Pope, Massac, Johnson, Pulaski, and Alexander counties before the Ohio River divided and shifted to assume its current more southern channel during the Pleistocene (Alexander and Prior 1968; Hutchison 1987). This shift is thought to have been caused by meltwaters of Wisconsinan glaciation 13,000 to 10,000 years ago (Alexander and Prior 1968; Hutchison 1987). The current floodplain of the Cache River now occupies the western portion of the old channel of the Ohio River (flowing into the current Ohio River near Cairo, Alexander County), while the lower drainage of Bay Creek occupies the eastern portion (flowing into the Ohio River near Bay City, Pope County).

In presettlement times the drainages of Bay Creek and the Cache River contained large floodplain swamps known as Big Black Slough and Little Black Slough (Hutchison 1987) that probably provided nearly continuous habitat for *H. avivoca* across this part of the state. Big Black Slough drained into the Cache River through a sluggish stream or received water



from the Cache River depending on flood level. During 1913–1916, Post Creek Cutoff, a shortcut to the Ohio River, was excavated by humans to carry water from the upper Cache River more quickly and reduce flooding of agricultural fields downstream. As a consequence, Big Black Slough and much of Little Black Slough were drained, timbered, and converted to agriculture leaving scattered populations of *H. avivoca* in remnants of original swamp. Thus, although the populations along Bay Creek and the Cache River might superficially appear to have ancient independent origins, their isolation actually is a recent result of human environmental alteration.

Elsewhere in the valleys of the Mississippi and Ohio rivers, *H. avivoca* is known from western Kentucky (Barbour 1971), western Tennessee (Redmond and Scott 1996), Arkansas (Trauth and Robinette 1990), Mississippi (Lohofener and Altig 1993), and Louisiana (Dundee and Rossman 1989; Fouquette and Dalahoussaye 1966), but has not been reported from Missouri (Johnson 1987) immediately west of some localities in Illinois.

Many of our biogeographic comments on the distribution of *H. avivoca* in Illinois also apply to *H. cinerea*. However, while *H. cinerea* is associated with Austroriparian swamps, it is not limited to them. We have considered three possible explanations for the currently expanding range of *H. cinerea* in Illinois: (1) construction of many new aquatic breeding habitats, such as farm ponds and impoundment reservoirs; (2) the ability of the species to colonize new aquatic habitats rapidly through dispersal of subadults; and (3) introduction of tadpoles through fish stocking into many of the new aquatic habitats.

### Range Expansion of *Hyla cinerea*

The range of *H. cinerea* is expanding in southern Illinois. The northernmost localities we found (Rockwood, Randolph County, and northwestern Kinkaid Lake, Jackson County) are both ca. 27 km farther north than Smith's (1961) northern range limit for the species. This species has the capacity to

invade new habitat through dispersal of offspring, since recently transformed juvenile *H. cinerea* have been found up to 0.5 km from the nearest breeding habitats (this study). It also is possible that previous surveys overlooked small, localized populations that have expanded during recent years. However, the increasing number of permanent impoundment lakes, retention ponds, and farm ponds constructed in southern Illinois since the 1950s has facilitated expansion of *H. cinerea* by providing additional suitable habitat. Many of these impoundments and ponds are stocked and managed for sport fishing. Predatory fishes may not exclude *H. cinerea* from these permanent aquatic habitats as they do some other amphibians. Blouin (1990) presented experimental evidence that tadpoles of *H. cinerea* are less vulnerable than tadpoles of *H. gratiosa* to predatory fishes (either through greater unpalatability or difference in behavior), and this may help explain the continued occurrence of *H. cinerea* in permanent lakes and swamps.

There is further evidence that human assistance has allowed *H. cinerea* to expand its range in Illinois. It is likely that fish farms on the floodplain of the Mississippi River were colonized by *H. cinerea* from nearby swamps, although it is possible that the fish farms were colonized by adults or tadpoles introduced with fish stock from other fish farms. It is pertinent also to consider how *H. cinerea* entered the medium to large reservoirs. Most are far from remnant swamps, but all periodically are stocked with fish. It is possible that tadpoles of *H. cinerea* were introduced along with fish raised in hatcheries. P. Reif, owner of a fish farm in Jackson County where we found *H. cinerea*, confirmed (pers. comm.) that tadpoles are included in deliveries of stock fish from his farm, although efforts are made to exclude them. While Reif was familiar with adult *H. cinerea*, he could not identify their tadpoles. Introduction of tadpoles through fish stocking probably is widespread. In 1991 and 1993, MR observed tadpoles of *R. catesbeiana* being introduced when catfishes (*Ictalurus punctatus*, *Pylodictus olivaris*), largemouth bass (*Micropterus salmoides*), and walleyes



(*Stizostedion vitreum*) were stocked into public fishing lakes in DuPage County, Illinois. All the fish and tadpoles originated from fish farms  $\geq 70$  km away. LEB also observed tadpoles of *R. catesbeiana* being introduced with fishes in the 1970s into the human-made impoundment Evergreen Lake, McLean County, in central Illinois. Furthermore, as *R. catesbeiana* has been introduced widely throughout much of western North America (Wright and Wright 1949; Stebbins 1951), it is logical to conclude that some (perhaps many?) of these introductions occurred as tadpoles through the numerous fish stockings that have taken place. In 1996 at the Aquaculture Facility, Illinois State University, B. Wainscott and P. Foley (pers. comm.) found a number of metamorphosing American toads (*Bufo americanus*) in a shipment of yellow perch fry (*Perca flavescens*) that originated from Cambridge, Wisconsin (ca. 292 km to the north). In 1997, E. Massarolo (pers. comm.) found significant numbers of tadpoles of *R. catesbeiana* in shipments of goldfish (*Carassius auratus*) and guppies (*Poecilia reticulata*) to a pet store in Bloomington, Illinois. Platz et al. (1990) presented evidence for the introduction of the Rio Grande leopard frog *Rana berlandieri* into southwestern Arizona from Uvalde, Texas, and eastern New Mexico. They implicated transport of eggs or tadpoles during fish stockings. Thurow (1994) intentionally established wood frogs (*R. sylvatica*) by introducing eggs, tadpoles, and adults (collected in Brown County, Indiana) into woodland pools in McDonough County, Illinois. Reinert (1991) and Thurow (1994) noted that introductions of early life stages were most likely to be successful in establishing new colonies.

There is considerable evidence that tadpoles occur in abundance in fish hatchery ponds. Brown (1971) studied reproductive ecology of Woodhouse's toad, *Bufo woodhousei*, and the Gulf Coast toad, *Bufo valliceps*, at a federal fish hatchery in Austin, Texas. Large numbers of both species of toads as well as *R. catesbeiana* laid massive numbers of eggs in the 19 hatchery ponds. (The *R. catesbeiana* were introduced by the hatchery management in hopes that they would prey on

the toads.) The hatchery personnel made persistent but unsuccessful attempts to eliminate the toads over many years. Eggs were killed by tossing them onto the banks, and adults were transported elsewhere or killed. This seemed to have had little effect because large numbers of toads returned to breed during the three-year study. LEB noted a similar abundance of tadpoles of American toads, *B. americanus*, in the fish hatchery ponds of Southern Illinois University at Carbondale in the early 1960s. W. Lewis (pers. comm.) also reported problems in the 1960s and 1970s with large numbers of anuran tadpoles in fish hatchery ponds near Gorham, Illinois (which is within our study area). Brown (1971) suggested that the filling of the ponds may be a factor that stimulates anurans to use them for reproduction. More recently there has been more extensive documentation that "tadpole infestation" is a serious problem in fish hatcheries (Carmichael and Tomasso 1983; Corse and Metter 1980; Gabbadon and Chapman 1996; Kane and Johnson 1989; Kane et al. 1985; Kane et al. 1992). Tadpoles often constitute 50–75% of the harvest biomass, and can reach over 2,000 kg/ha (Kane and Johnson 1989; Kane et al. 1985). Thus, there are ample indications that tadpoles occur in fish hatcheries, and that tadpoles are included in outgoing shipments of fish.

*Hyla cinerea* also may be expanding its range (either naturally or by introduction) elsewhere. Conant (1977) suggested that the isolated population(s) in the area near Brownsville, Texas, initially resulted from escapees from the pet trade. Snyder and Platt (1997) reported possible range expansion in South Carolina. An introduced population of *H. cinerea* was reported at a fish farm in Camden County, Missouri, by Johnson (1987) and recent records (Powell et al. 1995, 1996) from southeastern Missouri could indicate range expansion there. In 1974 a now-extinct colony was established at a fish farm in Douglas County, Kansas (Collins 1993; J. Parmelee, pers. comm.), and an introduced population is known in Puerto Rico (Schwartz and Henderson 1991).



### Conservation Biology

Smith (1961) reported *H. avivoca* from 3 localities in Illinois; we report it from 29 localities (of which 24 are documented by vouchers). The increase probably is due more to additional field work than to range expansion. This species occurs today only in remnant natural swamps, many of which currently are difficult to access, and certainly were even less accessible when Smith was surveying the state's herpetofauna. Twenty-one (72%) of the current localities are in the drainage of the Cache River, three (10%) are in the drainage of Bay Creek, and five (17%) are in the bottomland of the Big Muddy and Mississippi rivers. This species may have been extirpated from Olive Branch/Horseshoe Lake, Alexander County. Horseshoe Lake went dry in the summer of 1930 (Cahn 1937; Thompson and Bennett 1938), and that might have influenced the decline or extinction. Of greater significance may be the intensive long-term management of the lake for recreation by the State of Illinois, which has involved control of vegetation along the shore (M. Morris, pers. comm.). *Hyla avivoca* was heard only twice at another locality (Oakwood Bottoms/Worthen Bayou, Jackson County), where it may also be close to extinction or extirpated. All populations are in or along the margins of remnant baldcypress/tupelo gum swamps. Choruses were largest in less disturbed swamps where canopy cover was greatest and the understory well shaded at midday. Choruses were smallest where mature baldcypress and tupelo gum trees were sparse or dying and the canopy was more open. Similar observations were reported for choruses of *H. avivoca* in Oklahoma (Secor 1988). There also is evidence (based on diet) that *H. avivoca* forage in arboreal habitat, rather than on the ground (Jamieson et al. 1993; Redmer et al. 1999).

The management history of Horseshoe Lake clearly shows how habitat disturbances may have led to the decline of *H. avivoca* and other Austroriparian amphibians and reptiles. Horseshoe Lake is a cut-off meander, oxbow lake formed in the wide floodplain of the Mississippi River about 6,000 years ago

(Bogner et al. 1985). Sources of water for the lake originally were its 39.3-km<sup>2</sup> drainage, flooding from the Mississippi River, and rainfall. The 76-hectare lake (a seasonal slough before spillway construction) drained into the Cache River by way of Lake Creek. Stop log and concrete spillways were constructed on Lake Creek in 1927, 1931, and 1939 (Thompson and Bennett 1938), prior to which the meander had existed as a shallow baldcypress swamp that dried partially during July and August. Lake Creek is subject to annual spring backwater flooding from the Cache River and floodwater occasionally enters the lake over the spillway. Until 1969, when the Fayville Levee was completed, Horseshoe Lake occasionally received overbank flooding from the Mississippi River through Big Cypress Creek into Black Creek (Bogner et al. 1985; Lee 1993). Horseshoe Lake also is threatened by excessive sedimentation (Lee et al. 1986). During the flooding of the Mississippi River in 1993 and 1994, several months of inundation killed much of the surrounding forest, including many tupelo trees. Animal and plant life at Horseshoe Lake includes many Austroriparian species, making it one of the most distinctive natural areas in Illinois (Evers and Page 1977). In addition to *H. avivoca* and *H. cinerea*, Austroriparian amphibians and reptiles known to occur there historically include the mole salamander (*Ambystoma talpoideum*), Mississippi green water snake (*Nerodia cyclopion*), mud snake (*Farancia abacura*), broad-banded water snake (*Nerodia fasciata*), plainbelly water snake (*Nerodia erythrogaster*), and cottonmouth (*A. piscivorus*). These species thrive in shallow, bottomland baldcypress and tupelo swamps subjected to cyclic flooding and drying. They may have been negatively affected when the seasonal swamp was converted into a permanent lake in the late 1920s and early 1930s. Subsequently, Horseshoe Lake has been protected from most overland flooding of the Mississippi River and managed for the benefit of sport fishing and waterfowl. While a few Austroriparian species (*A. talpoideum*, *H. cinerea*, *N. erythrogaster*) remain locally common, the others are rare or



extirpated (Brandon et al. 1994; Heidinger et al. 1994, 1995; Brandon and Wilson 1996).

Twenty-three of the twenty-nine (79%) current known breeding sites for *H. avivoca* are owned in whole or in part by public (Illinois Department of Natural Resources, United States Forest Service [Shawnee National Forest], United States Fish and Wildlife Service [Cypress Creek National Wildlife Refuge]) or private (The Nature Conservancy) conservation agencies, so protection of most remaining habitat is possible. Nevertheless, because of the frog's dependence on scattered fragments of declining habitat, we formally recommended (while this manuscript was in preparation, 2 December 1997) that the Illinois Department of Natural Resources and Illinois Endangered Species Protection Board consider listing *H. avivoca* as a threatened species. The Board voted positively in August 1998 on this recommendation and the species is now listed as threatened in Illinois (Illinois Endangered Species Protection Board 1998). Additional studies will be necessary to determine micro-habitat requirements so that remaining habitats can be managed in a way that is beneficial to the frogs. Management may need to include cyclic manipulation of water levels to ensure that healthy stands of mature tupelo and baldcypress (as well as diverse understory) persist.

Smith (1961) reported *H. cinerea* from 4 localities in Illinois, whereas it is now known from 127. Although it occurs around the open edges of baldcypress/tupelo swamps, *H. cinerea* is not limited to them. It is less of a habitat specialist than *H. avivoca*, and often is abundant in a variety of disturbed, successional, or open swamp habitats, as well as sink ponds, farm ponds, borrow pits, and shallow bays of many constructed lakes. There is no evidence that *H. cinerea* is in danger of extirpation in Illinois.

With all the recent media publicity concerning the "decline of the Amphibia," it could be regarded as unusual that *H. cinerea* is significantly expanding its geographical range and increasing markedly in numbers. However, within historical times there have been major range expansions by at least two other

anurans: the bullfrog, *R. catesbeiana*, in western North America (Wright and Wright 1949; Stebbins 1951), and the giant toad, *Bufo marinus*, in Australia and elsewhere (Tyler 1989). Both of these colonizations were knowingly facilitated by humans (for sport purposes and consumption in the case of *R. catesbeiana*; for biological control of sugar cane pests in the case of *B. marinus*). The expansion of *H. cinerea* probably is natural and also unknowingly facilitated by human beings through inadvertent introductions of tadpoles with game fishes and creation of new habitat. Whether or not the expansion of *H. cinerea* will reach the magnitude of those of *R. catesbeiana* and *B. marinus* is unknown, but it presents a tremendous opportunity to study amphibian success and contrast it with species headed toward extinction. Such a comparison should increase our understanding of the decline of the Amphibia, and perhaps supplement our meager knowledge of how these important animals can be conserved.

## Summary

The bird-voiced treefrog (*Hyla avivoca*) and green treefrog (*Hyla cinerea*) are Austro-riparian species that reach the northern limits of their ranges in the Midwest in far southern Illinois. *Hyla avivoca* is a habitat specialist that persists only in remnant baldcypress/tupelo swamps, which were more widespread in former times. Its survival in Illinois depends upon the survival of this swamp habitat. *Hyla avivoca* is restricted to isolated colonies (often with low numbers of individuals) in drainages of the Big Muddy River, Mississippi River, Cache River, and Bay Creek in Alexander, Jackson, Johnson, Pope, Pulaski, and Union counties. Males call from a variety of emergent plants, commonly the trunks and branches of baldcypress and tupelo trees, nearly always over water. Tadpoles develop in cool, shaded water. Recently transformed juveniles and subadults often perch in low shrubs in nearby woods, on emergent shrubs, and on baldcypress and tupelo trees. In the fall they can be terrestrial.



*Hyla cinerea* occurs in a wide variety of disturbed, successional, and open swamp habitats, and during the past 30 years has been undergoing considerable expansion of its range into farm ponds, borrow pits, and shallow bays of reservoirs constructed since the 1950s. It is widely distributed across much of Alexander, Jackson, Johnson, Massac, Pope, Pulaski, and Union counties, as well as in parts of Randolph and Williamson counties. Males call from shrubs, small trees, and other emergent vegetation in a variety of wetland habitats sunlit by day in the open or under sparse tree canopy. Tadpoles are abundant in warm sunlit waters covered by mats of duckweed. Recently transformed juveniles are found in emergent vegetation, shoreline shrubs, and even nearby grassy fields.

Both species probably originally invaded southern Illinois by moving northward up the Mississippi embayment with subsequent colonization of the drainages of the Cache, Big Muddy, and Ohio rivers. Although the populations of *H. avivoca* along Bay Creek and the Cache River might superficially appear to have independent origins, their separation actually is a recent result of intervening human environmental alteration. The currently expanding range of *H. cinerea* in southern Illinois probably is a result of (1) construction of many new breeding habitats by humans (e.g., farm ponds, reservoirs), (2) the ability of dispersing metamorphosed young to colonize new aquatic habitats rapidly, and (3) introduction of tadpoles by humans through fish stocking into many new aquatic habitats.

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## Appendix

Locality data for *Hyla avivoca*, *Hyla chrysoscelis*, *Hyla cinerea*, and *Hyla versicolor* complex examined. Vouchers are listed in parentheses after localities. When a voucher is not listed, the individual(s) was (were) identified by mating call, photograph, and/or capture (with subsequent release).

***Hyla avivoca*:** Alexander Co., IL: Cypress Creek National Wildlife Area, Cache River just SE of Tamms (SIUC H-5379); Olive Branch, Horse Shoe Lake (FMNH 2201 [lot of 3]). Johnson Co., IL: 0.7 mi E of Grantsburg on Route 146 (SIUC H-5259-5260); Belknap Road just W of Cache River (SIUC H-5255); Bell Pond, W of Grantsburg on Route 146 (SIUC H-4741); Cache River bottoms, 1.6 km W of West Vienna (SIUC H-5257); Cache River State Natural Area, at Cache River and Route 37 (SIUC H-5254); Deer Pond Nature Preserve, ca. 0.3 mi N of old Route 146 (SIUC H-5382); Heron Pond, Little Black Slough (SIUC H-5123-5124); North Cypress access N of parking lot (SIUC H-5319); Route 37 at Cache River 0.9 km S of West Vienna (SIUC H-5248); Route 45 at Dutchman Creek bottoms ca. 1.25 mi N of Belknap Road (SIUC H-5270-5271); W of West Vienna and E of Route 37 (SIUC H-5122); W side of Cypress Pond State Natural Area (SIUC H-5258); Heron-Pond Little Black Slough, swamp south of Wildcat Bluff; Heron-Pond Little Black Slough, swamp west of Wildcat Bluff; Heron-Pond Little Black Slough, swamp NE of Hairy Hill; W side of Little Black Slough, E of Cypress (SIUC H-5262-5264). Pope Co., IL: 0.8 mi SE of Reevesville along Bay Creek floodplain (SIUC H-5251-5253, H-5383-5385); 1.5 km NE of Reevesville, along Sugar Creek (SIUC H-5543, H-5598 [tadpoles]). Pulaski Co., IL: Cache River State Natural Area, 0.25 km SW of Route 37 at Cache River bridge (SIUC H-5268); Cache River State Natural Area, 2 km NW of Karnak (SIUC H-5269); Limekiln Slough, 1/2-way between parking lot and spring (SIUC H-5381). Union Co., IL: 2 mi E Aldridge

(LSUMZ 6569); 2.5 mi E of Aldridge (SIUC H-661-662); 3 mi NE Aldridge (INHS 6062-6068); 5 mi N & 3 mi E Wolf Lake, Pine Hills, Recreation area (KU 63546); 5 mi SE Aldridge (INHS 3102 [lot of 2], 3312-3318, 4175-4179); 5 mi SE Aldridge (UIMNH 1725-1727); Hogan's Bottoms on Dongola Road just W of Cypress Creek (SIUC H-5216-5217, H-5256); La Rue Ecological Area (SIUC H-4387); La Rue Pine Hills Research Natural Area (SIUC H-5121); Pine Hills Recreation Area (ISM 626161-626166, 626171); Pine Hills, between SIU field station and Route 3 (SIUC H-2 [lot of 5]); swamp near Wolf Lake (UIMNH 95883-95884; UMMZ 95800, 95883-95884, 95885 [lot of 3]); Wolf Lake (swamp at base of bluffs) (SAM 104, 262-263); Wolf Lake (UIMNH 13074, 13076-13081, 70516); Wolf Lake swamps (SIUC H-1267).

***Hyla cinerea*:** Alexander Co., IL: 1.2 km SSE of Horseshoe Lake spillway (SIUC H-5289); Big Cypress Swamp (SIUC H-5292); Fayville Road 0.7 mi W of Olive Branch (SIUC H-4954-4955); Horseshoe Lake (INHS 1987, 5123; UIMNH 23897); Horseshoe Lake Conservation Area (SIUC H-3398, H-4661, H-4786, H-4813, H-4866, H-4938-4939, H-4969-4970, H-5007-5010, H-5146, H-5272, H-5275-5276, H-5280-5281, H-5191-5292, H-5294, H-5315-5316); Horseshoe Lake State Conservation Area on small cypress tree island, S side of West Side Dr. and Miller City arm of lake (INHS 12818-12819); old channel of Cache River just S of Tamms sewage disposal pond (SIUC H-5226, H-5473); Olive Branch (FMNH 6290 [lot of 8]); 0.3 mi NE Olive Branch (captured and released); 0.6 mi NE Olive Branch (captured and released); 0.3 to 2 mi SW Olive Branch on Miller City-Olive Branch Road, many sites (captured and released; DORs); Olive Branch, Horse Shoe Lake (FMNH 2199 [lot of 53]); Route 127 at S side of Mill Creek at Union County line (SIUC H-5162-5163); along Cache River SE of Frog City. Jackson Co., IL: Carbondale, Evergreen Terrace (MAM 826); Carbondale, SIUC campus (SIUC H-5152-5153); Etherton (swamp on east side of Hwy 127) (INHS 10617-10618); Etherton Swamp on Route 127



S of Murphysboro (SIUC H-3202-3205); Giant City State Park, north end near rappelling area (captured, photographed, released); Grimsby, intersection of Routes 3 and 149 (SIUC H-5150); Kinkaid Creek, first bend S Route 149 (heard choruses on several nights in early 1960s; now extinct due to habitat destruction from torrential overflow of Kinkaid Lake dam); Kinkaid Lake, south end near end of road (captured, photographed, released by J. Karnes); Lake Indian Hills sewage lagoon near Carbondale (SIUC H-5243); Kinkaid Lake Johnson Creek Recreation Area access road 1.1 km E of Route 151 (SIUC H-4439); Lake Murphysboro State Park (SIUC H-5147); Logan Hollow Fish Farm, Gorham (SIUC H-5149); Lovett's Pond (SIUC H-5223-5225, H-5265-5267); north side of middle of Lovett's Pond (captured, photographed, released); Malibu Mobile Home Park, Carbondale (SIUC H-5143); Oakwood Bottoms (MAM 691); Oakwood Bottoms Waterfowl Management Area (SIUC H-5141-5142); Route 3, 2 km S of intersection of Route 149 (SIUC H-5148); Route 151, 0.3 km N of Route 3 (SIUC H-4711); S side of Makanda (SIUC H-5144); Touch of Nature Fisheries Ponds, S of Carbondale (SIUC H-5352-5354); Town and Country Trailer Court, S edge of Carbondale (SIUC H-3349-3352, H-3965-3966, H-3968-3971, H-5218); Turkey Bayou area (MAM pers. comm.); Wides Village, Murphysboro (SIUC H-3974). Johnson Co., IL: farm pond 3 km NW of Vienna; weedy bay on SW side of Lake of Egypt; 0.4 mi N of Belknap Road on Route 45 (SIUC H-5238); 0.7 mi N of Belknap on Route 45 (SIUC H-5234); 1.6 mi NE of Karnak on Belknap Road (SIUC H-5240); Belknap Road 1.1 km N of Karnak railroad crossing (SIUC H-5245); Cypress Pond State Natural Area (SIUC H-5246-5247, H-5408-5413); Dutchman Lake boat launch (SIUC H-5242); Heron Pond State Natural Area (SIUC H-5151); old Cypress Road and 146, 1.3 mi W of Vienna (SIUC H-5241); old Route 146, 0.2 mi E of Dutchman Creek (SIUC H-5140)); Route 37, 0.1 mi N of Cache River (SIUC H-5244); Route 37, 0.5 km S of Cache River (SIUC H-5211); Route 37, 2.2 km SW of

West Vienna (SIUC H-5145); Route 146 along Bell Pond, 0.6 km E of Grantsburg (SIUC H-5213-5214); Vienna (INHS 2342 [lot of 4]); W edge of Little Black Slough SE of Cypress (SIUC H-5261). Massac Co., IL: Mermet Lake Conservation Area (SIUC H-3777, H-3814); SE edge of Mermet Lake Conservation area along Rt. 45; NE of Mermet Lake along Rt. 45; NW of Mermet Lake along Rt. 169; W side of Fort Massac State park; E edge of Fort Massac State Park; 4 km SE Unionville in Ohio River floodplain. Pope Co., IL: 1 km NW of Renshaw along old railroad bed (SIUC H-5387); 1 mi W of New Liberty on the Unionville Road (SIUC H-4450, H-5126); 1.5 km E of Reevesville (SIUC H-5376, H-5599); Barren Creek (SIUC H-4442); Bay Creek 0.8 mi E of Reevesville (SIUC H-5378); Smithland Lock and Dam road, 0.1-0.3 km W of Army Corps building (SIUC H-4443-4447, H-5127); farm pond 0.3 km S of Big Black Slough, along Rt. 145. Pulaski Co., IL: 50 m E of dock at lower Cache River access area (SIUC H-5128); along Limekiln Slough, 5.3 mi E Ullin (INHS 10611-10613); Belknap Road 0.2 km N of Karnak railroad crossing (SIUC H-5239); ca. 2 mi SW Pulaski (MAM pers. comm.); Cache River State Natural Area, 2 km NW of Karnak (SIUC H-5249); Post Creek Cutoff, NE side of Karnak (SIUC H-5377); Route 37 on S side of Cache River at Cache River State Natural Area (SIUC H-5129-5131); Route 37, 0.2 mi S of Cache River (SIUC H-5236); Route 51 at S edge of Ullin, at Cache River bottoms (SIUC H-5125); Route 51 on N side of town of Pulaski (SIUC H-5132-5133); Route 51, 3 mi N of Ullin (SIUC H-5136-5137); Sandusky to Pulaski road just E of Cache River (SIUC H-5138-5139); Shawnee College campus (SIUC H-4438); Cache River floodplain W of Mounds; large pond NE side of Mounds; along Cache River 6 km W of Villa Ridge. Randolph Co., IL: Route 3 at Rockwood (SIUC H-4710). Union Co., IL: 1.1 km S of intersection of Mt. Pleasant Road and Route 146 (SIUC H-5160-5161); 2.0 mi. N Wolf Lake (INHS 3923); 5.0 mi. SE Aldridge (INHS 3100); 5.0 mi. SE Aldridge (INHS 3949); Aldridge (INHS 3149-3150); along Cypress Creek (SIUC H-5215);



Hogan's Bottoms, just W of Cypress Creek (SIUC H-5154, H-5156; H-5158, H-5173-5180, H-5235); Morgan Pond (SIUC H-5168-5172); Mt. Pleasant, 0.3 mi S of Cache River (SIUC H-5157); Mt. Pleasant, 100 m S of main intersection (SIUC H-5166-5167); Old Cape Road 1.3 km E of Bluff Lake (SIUC H-4781-4783); Old Cape Road at 3rd bridge E of Route 127 (SIUC H-4722); Old Cape Road at Route 127 (SIUC H-5159); Pine Hills (SIUC H-62-63, H-72, H-77-78, H-188, H-653, H-1108, H-1676-1679, H-1900-1902, H-2673, H-3356-3365); Pine Hills Recre. Area (ISM 626071-626078, 626098); Pine Hills Swamp (INHS 2503-2505; ISU 1639, 1643, 1662, 1684, 1706); swamp near Wolf Lake (UMMZ 95796 [lot of 3]); Union County Conservation Area (SIUC H-4719-4721, H-5164-5165); Upper Bluff Lake along logging road on E side (SIUC H-5155); Wolf Lake (swamp at base of bluffs) (SAM 105); Wolf Lake (UIMNH 13028, 13030-13032); retention pond along Rt. 127 at Alto Pass; pond at Pine Hills campground; "State Pond" 3 km NW of Jonesboro; S half of Union County Conservation Area (large choruses throughout area); Cache River floodplain 1.5 km NW of Mt. Pleasant; pond on NW side of Dongola; sink hole 2 km SE Dongola. Williamson Co., IL: Crab Orchard National Wildlife Refuge, spillway road (SIUC H-4102); Grassy Bottoms Swamp along Crab Orchard Lake spillway road (SIUC H-5134-5135); Little Grassy Lake (SIUC H-4436); Crab Orchard Lake in weedy bay 2.5 km E of spillway; Crab Orchard Lake, in S half of grassy bay; W side of Little Grassy Lake at Touch of Nature Camp.

*Hyla chrysoscelis*: Alexander Co., IL: 0.3 mi SE Promised Land Rd., S of Horseshoe Lake (LEB 122 [lot of 3]); Horseshoe Lake Conservation Area (SIUC H-4807, H-5078). Franklin Co., IL: SW Zeigler (SIUC H-3802). Jackson Co., IL: Cedar Lake (SIUC H-3804); Giant City State Park (SIUC H-3794); Grand Tower (SIUC H-3801); N of Big Muddy River, W side of Route 3 (SIUC H-71 [lot of 7]). Johnson Co., IL: Cypress Pond State Natural Area (SIUC H-5707-5709); Ferne Clyffe State Park (SIUC H-3800); Grantsburg (SIUC H-81

[lot of 11]). Massac Co., IL: near Cagle Pond (SIUC H-3799). Pope Co., IL: ca. 1 mi W of New Liberty on Unionville Road (SIUC H-4951-4952); Ohio River Recreation Area near Golconda (SIUC H-3796); One Horse Gap (SIUC H-3798). Saline Co., IL: N Carrier Mills (SIUC H-3803). Union Co., IL: Giant City State Park (SIUC H-3793); Trail of Tears State Forest (SIUC H-3795). Williamson Co., IL: Crab Orchard National Wildlife Refuge (SIUC H-3792).

*Hyla versicolor* complex: Jackson Co., IL: Murphysboro (FMNH 25940). Madison Co., IL: no specifics (USNM 57827). St. Louis Co., MO: St. Louis (USNM 3667 [lot of 4], 104553).

*Hyla* sp. (*H. avivoca* or *H. versicolor* complex): Alexander Co., IL: Horseshoe Lake (LSUMZ 51046). Union Co., IL: Ware, Union Co. Wildlife Refuge (LSUMZ 51047).















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